THE CLASSIFICATION OF THE ARTHROPODA.

By J. S. Kingsley.

In the concluding section of my paper on the Embryology of Limulus ('93), I expressed my views upon the classification of the Arthropods. The following is to be regarded as an expansion of the remarks I then made, with the inclusion of some matter not then available.

Since the days of von Siebold ('46), the naturalness of the group of Arthropoda has been almost universally recognized, only a few, like the present writer ('83) and von Kennel in his recent text-book of Zoology ('93), appearing to doubt the homogeneity of the division. On the other hand, the way in which the Arthropoda should be subdivided has been very differently regarded by different authors. Space will not permit an extended résumé of the growth of our knowledge, but it is fair to say that almost every person treating of the subject has added materially to the basis for a natural classification, either by the discovery of new facts or by throwing new light upon facts known before. At present, the great majority of naturalists divide the Arthropod phylum into two groups or sub-phyla, which, however named, are essentially Branchiata and Tracheata, the former embracing the Trilobites, Eurypterids, Hemiaspids and Xiphosures, along with the true Crustacea; the latter containing the Onychophora (Peripatus) Myriapods, Hexapods and Arachnids.

Yet this division is not universally accepted, and a few years ago, Professor E. Ray Lankester, following out the earlier suggestion of Strauss-Dürckheim and the later one of the younger van Beneden ('71), demonstrated that the affinities of Limulus were with the the Arachnids rather than with the Crustacea. This epoch-making paper—" Limulus an Arachnid "—must form the basis of all farther studies of Arthropod taxonomy, since it logically follows from his conclusions that the distinctions made between Branchiata and Tracheata are physiologi-

cal rather than morphological, and that their emphasis tends to obscure true relationships upon which alone a natural system can be based. Since Lankester wrote, most students of Arachnid morphology and every one (excepting Professor Packard) who has investigated the structure or ontogeny of Limulus, have endorsed the general conclusion that Limulus is closely related to the Arachnids.

This being the case, Lankesters's later views upon the subdivision of the Arthropoda possess a peculiar interest. In the ninth edition of the Encyclopedia Britannica, article "Zoology," he gives the following arrangement:

Branch Arthropoda.
- Grade 1, Ceratophora.
  - Class I, Peripatidea.
  - Class II, Myriapoda.
  - Class III, Hexapoda.
- Grade 2, Acerata.
  - Class I, Crustacea.
  - Class II, Arachnida.
  - Class III, Pantopoda,
  - Class IV, Tardigrada.
  - Class V, Linguatulina.

Professor Claus is apparently not so radical in his ideas. I fail to make out from his various polemical articles ('86 [a, b]., 87 [a]) exactly what his later views are, but in the fourth edition of his Lehrbuch ('88)—the fifth edition is not at hand —there is such a lack of regularity in the subordination of type, headings, etc., that it is difficult to ascertain his opinions. As I interpret him, he has the following scheme:

Arthropoda.
- Class 1, Crustacea.
  - Sub-Class I, Entomostraca.
  - Sub-Class II, Malacostraca.
  - Gigantostraca.
    - Merostomata.
    - Xiphosura.
- Class II, Arachnoida.
- Class III, Onychophora.

Class IV, Myriapoda.
Class V, Hexapoda.

From this it would seem that the only conclusions which can be drawn are that, at least at this date, Professor Claus regarded the Gigantostraca as a subdivision of the Crustacea, but was uncertain whether to regard it as equivalent to the Entomostraca and Malacostraca or not.

It is impossible to give the views of Hatschek, as the part of his " Zoologie " treating of the Arthropods has not yet appeared. In his general table ('88, p. 40) he accepts, in a modified way, the Articulata of Cuvier, and regards the Onychophora as a class, of equal rank with the Arthropoda.

The earlier studies of Boas upon the classification of the Crustacea possess such value that his general ideas upon the subdivisions of the Arthropoda deserve mention. In his " Zoologie " ('90) he adopts the following arrangement:

Arthropoda.
- I Class, Crustacea.
  - I Sub-Class Entomostraca, including as Orders: I, Phyllopoda; II, Cladocera; III, Xiphura (*sic*); IV, Trilobitæ; V, Ostracoda; VI, Copepoda; VII, Cirripedia.
  - II Sub-Class, Malacostraca.
- II Class, Myriapoda.
  - (Peripatus doubtful.)
- III Class, Insecta.
- IV Class, Arachnida.

Lang ('88) has the following classification:

Arthropoda.
- I Sub-Phylum, Branchiata.
  - Only class Crustacea.
    - First "Anhang to Branchiata—Trilobita, Gigantostraca, Hemiaspidæ, and Xiphosura.
    - Second "Anhang"—Pantopoda.
- II Sub-Phylum, Tracheata.
  - I Class, Protracheata.
  - II Class, Antennata (Myriapoda and Hexapoda).
  - III Class, Chelicerotæ *sive* Arachnoidea.
    - "Anhang" to Arthropoda—Tardigrada.

Fernald has approached the subject from the standpoint of Hexapod morphology. He gives ('90) a phylogenetic tree in which two main trunks arise from the primitive unsegmented worm. One of these embraces the Annelids and Peripatus, the other includes the Arthropods proper. This latter branches into the Hexapods and the Crustacea, the Arachnids and Limulus being represented as offshoots from the main Crustacean line. The origin of the Myriapods is left in doubt, but of the two divisions the Chilopods are represented as an offshoot from the Diplopod stem.

Richard Hertwig ('92) adopts the following scheme:

Branch Arthropoda.
- I Sub-Phylum, I Class, Crustacea.
  - 1 Sub-Class, Entomostraca, containg as regular members the Orders: I, Copepoda; II, Branchiopoda; III, Ostracoda; IV, Cirripedia; and, as "Anhangen," V, Xiphosura; VI, Trilobitæ; VII, Gigantostraca.
  - II Sub-Class, Malacostraca.
- II Class, Onychophora.
- III Class, Myriapoda.
- IV Class, Arachnoida (including Pantopoda as an "Anhang").
- V Class, Hexapoda.

Lastly, von Kennel, whose studies on Peripatus entitle his views on Arthropod taxonomy to a hearing, denies ('93) the validity of the group Arthropoda, claiming that those features which would seem to unite the Tracheata and Branchiata are either superficial or are common to the whole series of metameric Invertebrata. He places the Xiphosura among the Crustacea, apparently regarding them as equivalent to the rest of the group. The Tracheata are divided into three sub-classes, Myriapoda, Hexapoda and Arachnoida, the relationships of Tardigrada and the Pycnogonida being regarded as uncertain.

My own views, as stated in my last paper on Limulus, have not undergone any extensive modification, although the tabular statement has undergone some slight changes. Chief of these is the transfer of the Trilobitæ from a position of uncertainity to a more close union with the true Crustacea, a matter

which will be referred to again below. I would now present the following scheme:

Phylum Arthropoda.
  Sub-Phylum I, Branchiata.
    Class I, Crustacea.
      Sub-Class I, Trilobitæ.
      Sub-Class, II, Eucrustacea.
    Class II, Acerata.
      Sub-Class I, Gigantostraca.
      Sub-Class II, Arachnida.
  Sub-Phylum II, Insecta.
    Class I, Chilopoda.
    Class II, Hexapoda.
  Sub-Phylum III, Diplopoda.
Incertæ Sedes—
  Pycnogonida.
  Linguatulina.
  Pauropoda.
  Tardigrada.
  Malacopoda.

The various papers by Lankester, McLeod, Laurie and myself have, I think, clearly shown that the older grouping of the Arthropoda into Branchiates and Tracheates is not justified by the facts of structure and ontogeny; that tracheæ are not homologous structures in all Arthropods which possess them, and that the old group of Tracheata is polyphyletic in origin. Since classification must represent the various lines of descent, the old must therefore go. There remain many points which must be investigated anew, but I feel confident that further research will support, in its main features, the classification adopted above, and considered more *in extenso* below.

PHYLUM ARTHROPODA.

I am not prepared to discuss the validity of this group, although for reasons that will appear below, I am inclined to believe the great divisions which I recognize are but remotely related to one another, and it may yet be proved, as I suggested several years ago ('83), and as von Kennel believes, that

they have no common ancestor nearer than the Annelids. The jointed nature of the appendages offers no insuperable objection to this view, while the early phases of the egg, the formation of the germ layers, the structure of the alimentary canal, the morphology of the reproductive and excretory organs, as well as certain facts concerning the circulatory, respiratory and nervous systems are easiest explained upon such an hypothesis. The presence of compound eyes in branchiate and tracheate forms would, at first thought, be a strong argument for the older views, but these organs differ so greatly in their structure that it is easier to regard them as homoplastic organs (comparable in a way to the eyes of Cephalopods and Vertebrates) rather than as derivatives from a common compound ancestral visual organ. For our present purposes, the group of Arthropoda may be retained as a convenient assemblage, characterized in the following manner: Heteronomously segmented animals, with, typically, a pair of appendages to each somite; the whole enclosed in a chitinous segmented exoskeleton, the jointing of which extends to the appendages, thus justifying the term Arthropoda. The appendages, primitively locomotor in function, may be modified, on one or more somites, for the taking or commuting of food, for respiration, copulation, oviposition, sensation, fixation, etc. No circular layer of muscles in body wall; nervous system consisting of a pair of primitively supraœsophageal ganglia and a ventral chain of paired ganglia, of which one or more pairs may, in the course of development, be transferred to the prestomial region. Eyes, simple, aggregate, or compound, with, in some cases, an inversion of the retinal layer. Cœlom small, inconspicuous; circulatory organs consisting of a dorsal heart enclosed in a vascular pericardial sac; blood-vessels more or less evidently metameric, terminating in "lacunar" spaces. Respiration, either by the entire surface of the body or by specialized outgrowths or involutions of the same. Excretion, either by true nephridia or by Malpighian tubules, developed from either the mid- or the hind-gut. Reproductive organs consisting of gonads developed from the cœlomic walls and with modified nephridia serving as efferent ducts.

In order that we may compare, part with part, the different forms of Arthropods, it becomes necessary to assume some basis of comparison, and apparently the only one available is that of the exact homology of the similarly situated meta meres in the different groups, but here we meet with a difficulty. How can we be certain, for example, that somite 10 of the lobster is the exact homologue of somite 10 in the beetle? How can we tell that no somite has been lost in the evolution of these different lines? Perfect certainty is impossible, and we now know that in the serial comparisons of not more than five years ago, errors crept in, because there is a tendency of somites to become aborted or obsolete. This tendency is well-known in cases of Apus and Oniscus, where one of the anterior pairs of appendages is greatly reduced; and in Limulus, Scorpions, Moina, etc., where an anterior somite is not differentiated until after those behind it. In many forms there is an obliteration or a fusion of cœlomic cavities in the anterior region, the mesoderm flowing together as a common mass.

On the other hand, the embryonic phases of the nervous system seem to give clear indications of neuromeres in the anterior end of the body, and, as farther back, neuromeres correspond to the mesodermic metameres, it is reasonable to accept until error be shown, a somite for each neuromere at the anterior end of the Arthropod body. Unfortunately, we have detailed knowledge of these neuromeres in but few cases, and even in these there is a lack of uniformity in the observations.

In the Hexapods it has been shown that the "cerebrum" of the adult is composed of at least three pairs of ganglia called by Vaillanes, respectively, the protocerebrum, the deutocerebrum and the tritocerebrum. These elements have been recognized by Tichomiroff in the silkworm (teste Cholodkowsky) in Acilius (Patten, '88), in Blatta (Cholodkowsky, '91), in Mantis (Vaillanes, '91), in Xiphidium and Anurida (Wheeler, '93), while Carrière ('90) has described *four* cerebral elements in Chalicoderma. The figures of the latter author do not seem to me conclusive, and I am inclined to believe the more numerous observations in this difficult field as the more probably correct.

These cerebral elements apparently have different values. So far as observations go, the protocerebrum is always preoral, and in no case is any appendage developed in connection with it. Apparently, the region in which it occurs is to be compared to the preoral lobe of the annelids, while the two ganglia of which it is composed would correspond to the "Scheitelplatte" of German embryologists. The other cerebral elements, on the other hand, are primitively behind the stomodæum, and, in some forms at least, an appendage is developed in connection with each. Thus the antennæ belong to the deutocerebral neuromere, while in Anurida Wheeler has shown that the tritocerebral neuromere possesses at an early stage a pair of small appendages, which here, as in all Hexapods, is absent from the adult.

In the Crustacea, not a few observations go to show somewhat similar conditions. We find there a protocerebrum without appendages at any stage, followed by a series of ganglia which present many claims to belong to the postoral series. In a paper on the Embryology of Crangon ('89), I claimed that in that form the antennæ were primitively postoral, but since the validity of my observations have recently been questioned by Weldon ('92) and Herrick ('92),[1] they must be repeated before they can be accepted. Aside, however, from these questionable observations, there are many other facts which go to show that the antennal neuromeres belong to the the postoral rather than to the prestomial series. There is, however, less evidence for this position for that pair of ganglia which exist in the lobster (see Bumpus ('91), pl. XVII, fig. 1), between the protocerebral ganglia and the neuromeres of the antennæ. It is without appendages, and although its fate has not been traced, it probably becomes fused in the "cerebrum" of the adult.[2] This neuromere is, I am inclined to think, also to be regarded as belonging to the same series as that of the antennæ.

[1] For some remarks upon these criticisms, see my paper ('93), p. 235, foot-note.

[2] Professor J. P. McMurrich informs me that he has found these deutocerebral ganglia in the various Isopods (Jæra, Oniscus, Porcellio, Armadillidium, etc.) which he has studied.

In the Arachnids and the Xiphosures, we have evidence of several elements in the "brain." Both Patten and myself have shown the existence of three pairs of cerebral ganglia in Limulus, in front of the ganglia of the first pair of appendages. Patten finds ('90) the same number in the brain of the Scorpion, as do Locy ('86, pl. XI, fig. 70) and Kishenouyi ('90) in Agalena. The copies of Morin's figures given by Korschelt and Heider ('92, fig. 383 B) seem also to be in full harmony. On the other hand, Schimkewitsch (87, pl. XXI, fig. 3) represents two pairs of ganglia in Epeira in front of the ganglia of the first pair of appendages, while in the diagrammatic figure (pl. XXIII, fig. 5) he apparently indicates four pairs of preappendicular ganglia.

In other groups of Arthropods I know of no detailed observations which can be used to aid in the enumeration of the neuromeres in the anterior region of the body. If we assume that in the cases of Hexapods, Crustacea, Xiphosures and Arachnids, the neuromeres enumerated above represent the total somites in this region, we may then compare, somite by by somite, these groups in the following manner:

	HEXAPOD.	ARACHNID.	XIPHOSURE.	CRUSTACEA.
Neuromere I	No Appendage	No Appendage	No Appendage	No Appendage
" II	Antenna	No Appendage	No Appendage	No Appendage
" III	Appendage	No Appendage	No Appendage	Antennula
" IV	Mandible	Chelicera	1st Leg	Antenna
" V	Maxilla	Pedipalpus	2d Leg	Mandible
" VI	Labium	1st Leg	3d Leg	Maxilla 1
" VII	1st Leg	2d Leg	4th Leg	Maxilla 2
" VIII	2d Leg	3d Leg	5th Leg	Maxilliped 1
" IX	3d Leg	4th Leg	6th Leg	Maxilliped 2

Of course it will be understood that this grouping is limited by our present knowledge, and that at any time discoveries may be made which will overturn it. It is, however, to be noted that it brings the hinder margins of the thorax of the Hexapoda and of the cephalothorax of Limulus and of the

Arachnids into exact correspondence. In the case of the Crustacea the corresponding line passes behind the third maxilliped of the Decapod.

If it should, however, be shown (as many believe) that the Crustacean metastoma has its own somite, the line will be thrown forward to behind the second maxilliped, and it will correspond to the line of division between the head and thorax of the Edriophthalmia.

Since the older ideas of numerical sequence are better known, I have used them in the following discussion rather than that based upon the neuromeres. Thus in the Hexapods somite (or appendage) I=Neuromere II; in the Arachnid and Xiphosures somite I = Neuromere IV; in the Crustacea somite I = Neuromere III.

The morphology of some other organs call for a moments' consideration. Prominent among these are the vasa Malpighii. These are usually regarded as characteristic of the "Tracheates," and their presence in the Arachnids has been adduced as a strong argument for their association with the Hexapods. It has been, however, pretty conclusively shown that these organs are not homologous throughout the Arthropod phylum, for in the Hexapod they are derived from the hind-gut, and are therefore ectodermal, while in the Arachnida, as Loman ('86–7) has shown, they are derivatives of the mesenteron and are consequently entodermal. Their similarities are those of homoplassy rather than of homology, and the only argument that can be drawn from the occurrence in these forms is that Arachnids and Hexapods are not closely related. Similar organs with similar functions have been described in various Edriophthalmia, but we are yet in doubt as to their origin. The studies of Spencer ('85) represent them as without chitinous intima in the Amphipods. They may, therefore, be entodermal. A detailed study of the region of the hind-gut of certain Decapods might give results interesting in this connection.

The tracheæ furnished another instance of homoplassy. These organs furnish the chief ground for the group called "Tracheates," since in most they form the sole means of res-

piration. Yet these are, in the opinion of many, not homologous. In the Hexapoda they arise, ontogenetically, as inpushings of the ectoderm of sides of the body, outside and above the line of the insertion of the limbs. Their method of growth, the general structure, etc., all point to their origin, as was pointed out by Chun ('75) from dermal glands which later assumed respiratory functions. The tracheæ of the Arachnids, on the other hand, have had a different origin. In those forms in which they have been studied, they arise as inpushings behind the temporary appendages on the abdomen. There is not a little evidence to show that they have arisen from gills borne on the posterior surfaces of these appendages, as in the Limulus of to-day; that they have been pushed into the body, taking the form of lung books, a condition permanent in all the respiratory organs of the Scorpions and in those of one or two somites of the Araneina; and then, coincidently with a reduction in the circulatory organs, they have penetrated farther and farther into the body. For the details of this process, as well as for the wonderful histological similarity between the embryonic gills of Limulus and lungs of Arachnids the reader is referred to my full paper. The "spiral threads" in the two cases are to be explained as mechanical in origin—corrugations give greater strength without excessively thickening the intima. Still, a third type of "trachea" is to be be found in the gills of the Oniscid Crustacea. These organs have become adapted for aerial respiration, and, in connection with this change, the organs have been permeated by branches of minute tubes, lined with a chitinous intima, produced by inpushings of the outer body wall. These tracheæ cannot be regarded by the strongest advocate of the naturalness of the "Tracheates" as homologous (*i. e.*, homogenous) with those of the Hexapods. I have made a number of, as yet unpublished, observations on these organs in Porcillio. Leydig described them in detail some years ago ('78). The peculiar structures in the genus Tylos as described by Henri Milne-Edwards ('40, p. 187–8) should be considered in this connection.

It is only recently that the existence of nephridia in the Arthropoda has been placed beyond a doubt. The earlier students

of the shell gland of the Entomostraca often made comparisons between it and the "segmental organs" of the Annelids, but the trouble was that the former terminated blindly internally, while in the Annelids the organ formed a tube connecting the body cavity (cœlom) with the interior. The problem was solved by Sedgwick ('88), who showed that in Peripatus the nephridia were closed internally, but that they were still nephridia as proved by development, and that we have here to deal with a greatly diminished cœlom. In the light of these facts it is now placed beyond a doubt that in the antennal and shell glands of the Crustacea, and in the coxal glands of Arachnids and Limulus, we have true nephridia.[3] In all there is the formation of a cœlom, a division of the cœlom of certain somites into dorsal and ventral moieties, and a development of the lower portion into end sac and nephridial tube, the latter portion breaking through to the exterior.[3]

Following the discoveries by Sedgwick that the genital ducts of Peripatus were modified nephridia, came the observations of Heymons ('90), Cholodkowsky ('91) and Wheeler ('93), all of which show that exactly the same conditions exist in the Hexapods, while Laurie ('90) has demonstrated that it is at least probable that the same holds true for the Scorpions. I made no observations on the origin of the genital ducts of Limulus, and I do not recall any account of their development in the Crustacea. In the latter group, however, there is not a little evidence of an anatomical character which is easiest interpreted upon the same hypothesis. There these ducts are metameric, and may occur in different somites in the different sexes. This condition is to be explained in two ways, as has previously been pointed out by Lankester. Either the ducts are to be regarded as new formations, or they are previously existing structures modified for reproductive functions exclusively. That this latter is the case, and that the ducts are nephridial is rendered probable by the following considera-

[3] These organs have been shown beyond a doubt to be mesodermal by Grobben ('79, Kingsley ('89, '90 and '93), Kishenouyi ('91), Lebedinsky ('92), Laurie ('90), etc., and yet Bernard ('93), with these facts available, has recently attempted to derive these structures from the glands of annelids—ectodermal structures—ignoring the facts presented by those who have actually investigated the subject.

tions: In all metameric animals one or more pairs of nephridia serve as genital ducts, and no case is known of the formation of new outlets. The genital ducts are so related to the gonads and these latter to the cœlom, at least in the Decapods (*cf.* Weldon, '89, '91) that we must regard the genital epithelium as cœlomic, and the ducts as ventral diverticula of the same space.

The salivary glands afford some difficulties, for they occur in most "Tracheates," and are usually stated to be absent from the "Branchiates." This apparent difference between the two groups is possibly to be explained by the different method of life—aquatic in the latter, terrestrial in the former. It is, however, to be noted that salivary glands have been recognized in Astacus (*cf.* Lang, '89, p. 344), while renewed studies must be made of the so-called salivary glands of the Arachnida before we are certain of their homology with those of the Hexapods. Several organs which have been called salivary glands among the spiders and their allies have been shown to be coxal glands (*i. e.* nephridia) or poison glands, and it is possible that all of these organs may have different homologies than those indicated by the name usually applied to them.

A group of structures which cannot, as yet, be discussed, is that of the embryonic membranes. In the Scorpions as in the Hexapods, the embryo develops those as yet unexplained fœtal membranes which so closely simulate those of the higher vertebrates. It may be that here, as in other places, we have similar but not identical organs. The accounts of their development in the Arachnids by Metschnikoff, Kowalevsky and Schulgin, and Laurie differ considerably, and, until we know something of the ancestry and real meaning of the structures which are united under this head we cannot be certain of the taxonomic value to be placed upon them. It may be noted here that the structures described by Bruce ('87) as occurring in the spiders are, in all probability, not amnion and serosa, but either invaginations in connection with the brain or the inpushing to form the median eye.

SUB-PHYLUM I—BRANCHIATA.

Arthropods breathing by means of gills (or lungs or tracheæ modified from gills) developed in connection with the appendages; without distinctly differentiated head, with long stomodæum, nephridia persisting in somite II or V (or both), genital ducts opening near the middle of the body. Anterior appendages all multiarticulate, the basal joints of one or more pairs serving as organs of manducation. A chitinous entosternite and deutova frequently present.

I hardly think it necessary, each time the limits of a group are changed, to give the new combination a new name. Our nomenclature is already cumbersome enough, and the slight indefiniteness is vastly preferable to the confusion of the other course. I have, therefore, retained the term Branchiata for the enlarged group, since I regard the lungs and tracheæ of the Arachnids as but modified branchiæ. In only the Edriophthalmia and certain Phyllopods do we have a distinctly differentiated "head," and the head in these groups is not the same in its limits. Under the head of nephridia I include the antennal and shell glands of the Crustacea and the coxal glands of the Arachnids and Limulus. The former have been shown by numerous observers to be true nephridia, while the observations of Laurie ('90) and Lebedinsky ('92), Sturanay ('91), are conclusive to the Arachnids. The observations of Gulland ('85), Kishenouyi ('91) and myself ('85 and '93) would seem to settle the matter in the Horse-shoe crab.[4] That the genital ducts are to be regarded as modified Nephridia has already been shown. Their position is inconstant in the Crustacea, varying in some forms with the sexes of the same species. In some of the more reduced forms, as the cirripeds, they are apparently almost terminal, a condition to be explained by the

[4] In my first paper on the development of Limulus, I pointed out that the coxal glands of Scorpio and Limulus were apparently homologous with the shell gland of the lower Crustacea, since in both cases they open at the base of the fifth pair of appendages. This identification is apparently not pleasing to Professor Claus ('86, since he has seen fit to ridicule my ideas of homology. I confess that I do not understand his objections, and certainly the evidence derived from the neuromeres (admitting one for metastoma of the Crustacea—*cf.* Brooks, '82), seems fully to support my thesis.

small number of metameres that become differentiated. Other features which are common to most Branchiates, but which either are not common to all or are at the same time common to some of other groups, will appear below. It must, of course, be understood that in the above diagnosis of the group, features of internal anatomy are known only of recent forms; of the visceral structure of the trilobites, we are absolutely in the dark.

CLASS I—CRUSTACEA.

Branchiate Arthropoda with functional gills; with one or two pairs of distinctly preoral appendages (antennæ) the first being purely sensory; the ganglia corresponding to these appendages being fused with the protocerebrum to form the "brain;" the appendages with typically a basal joint giving rise to two or three branches; several pairs of appendages modified for eating; alimentary canal with long œsophagus and well-developed stomodeal "stomach," mid-gut region short, the mid-gut glands ("liver") being well-developed; proctodeum long.

In all living Crustacea (Eucrustacea), there are two pairs of antennæ, although in some forms (e. g., Apus, Oniscids) one or the other pair has has become greatly reduced. In the Trilobites, on the other hand, but a single pair has, as yet, been discovered. It therefore remains to be shown whether a single pair is characteristic of these forms, or whether we have here a possibly greatly reduced additional pair. In case the former alternative prove true, it may be necessary to remove the Trilobites completely from the position here assigned them, though it will not necessarily follow that they should be associated with the Eurypterids and Limulus. (For the position of the Trilobites, see below).

It is difficult to say exactly what weight should be given the so-called "typical Crustacean limb," the di- or trichotomous appendage so frequently met with in this class, and which is not infrequently regarded as diagnostic. That this condition is a derivation of the lamellate condition found in Apus, as maintained by Lankester ('81) admits of little doubt, and

hardly more doubtful is the view which would compare the Phyllopod appendage with the Annelid parapodium. But two- and three-branched appendages are not unknown outside the Crustacea. One of the arguments advanced in favor of a Crustacean position for Limulus is that the abdominal appendages in that form are two-branched, while numerous observers have recorded a biramous condition in the appendages of the young of various "Tracheates." Among others we would mention the biramous pedipalps in Dendryphantes recorded by Croneberg ('80), the biflagellate antenna of an Indian Lepisma, and of an embryo *Blatta javanica* by Wood-Mason ('79), the bifid condition of the antenna of Blatta by Wheeler ('89), while Patten ('84), in the same form, describes the maxillæ and labium as "formed respectively of two and three branches, the second maxillæ thus attaining the typical trichotomous structure of the Crustacean appendages." Similar observations have been made upon other Hexapods, while in the Pauropida the trichotomous antennæ are to be called to mind.

Fully as characteristic is the extreme reduction of the entodermal portion of the alimentary canal proper, the entoderm cells being largely confined to the liver or mid-gut gland, while the canal itself is almost entirely composed of stomodeal and proctodeal invaginations (*cf* Kingsley, '89, pp. 13-19).

SUB-CLASS I—TRILOBITÆ OR PALÆOCARIDA.[5]

Fossil Crustacea with tri-regional body—head, thorax, pygidium, all bearing appendages. "Head" unsegmented, with one pair of antennæ and with four pairs of postoral appendages, all pediform and with basal points manducatory. Thoracic somites indefinite in number, each bearing a pair of biramous (exopodite and endopodite) appendages, each appendage provided with a straight or curiously coiled gill (?). Pygidium segmented, with appendages beneath.

For several years I have maintained that the Trilobites had but the most distant affinities with the Xiphosures (e. g., '85, p. 555).

[5] This term was introduced by Packard ('79) for Limulus, the Trilobites and the Eurypterids. Later ('86), with no apparent reason, he dropped this term and substituted for it Podostomata. The two groups, as he limits them, are exactly the same.

In my latest paper ('93, pp. 252–254) I repeated the same ideas, and, within a short time of this paper, appeared Mr. Matthew's notice ('93) of the existence of true Crustacean antennæ in these forms. This, combined with the truly Crustacean thoracic appendages already described by Wolcott ('81 and' 84), and the utter inability, upon careful analysis, to homologise the regions in Limulus and the Trilobites, is sufficient to divorce the two and to assign the latter to the Crustacea.

Exactly what position they should occupy here is uncertain. It is undeniable that they present a superficial resemblance to the Isopoda. In both there is the same depressed body, the division of this into the three regions of head, thorax and abdomen, the head in both cases bearing sessile compound eyes; but at this point the resemblance ceases. In the Isopod the thorax is always 7-jointed; in the the Trilobites the number varies very considerably. In the Trilobites the appendages, as restored by Walcott, surround the mouth, much as in Limulus or the Scorpions; in the Isopods the arrangement is truly Crustacean. In the Isopods, in the embryo, as well as in the adult, the thoracic appendages consist of but a single branch, and when any other structures are present, as for instance, the plates forming the brood-pouch, these are placed mediad to the insertion of the limb; the gills (?) in the Trilobites are outside the point of articulation, while the limbs, as already stated, are dichotomously branched. In the Isopods the respiratory organs are lamellar appendicular plates beneath the abdomen; we do not know exactly what structures are found here in the Trilobites. Professor Mickleborough ('83) thinks that there are lamellar plates, but Mr. Walcott ('84) studying the same specimens believes that the appendages of this region resemble those of the thorax.[6] So it would appear that the Trilobites have no close affinities with the Isopoda; the resemblances to the Amphipods are even less close. So far as I am aware, there is no recent Crustacean which presents any resemblance to Trilobites closer than those of the Edrophthalmia just discussed, and yet we

[6] The process cuts illustrating Mr. Matthew's article gives no intelligible details of the foot structure in Triarthrus.

must consider these forms considerably removed from the primitive Crustacean stock, which, in the opinion of many, was not far removed from the modern Phyllopoda. Both types are well differentiated in the lower Cambrian, and no fossils as yet discovered serve to bridge the gap between the two. Nor does the little known of Trilobitan embryology throw any light upon the question. In some there is an apparent close similarity to the early stages of Limulus, but this may easily be explained upon the general principles of Arthropod growth. Thus, in Sao, as described by Barrande ('52), in which the resemblance to the Xiphosures is most marked, we have but that increase in the number of somites from a posterior budding zone common to most Arthropods, while in Trinucleus (Barrande) there seems to have been an acceleration in the development of cephalic and pygidial regions, and then, later, an increase in the number of thoracic segments in that manner so familiar in the development of the Decapoda. The resemblances to Limulus all lie in the depressed body form and the union of the anterior somites.

(*To be continued.*)